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Exploring species and site contributions to beta diversity in stream insect assemblages

Jani Heino[1] and Mira Grönroos[2]

[1]Finnish Environment Institute, Natural Environment Centre, Biodiversity, Paavo Havaksen Tie 3, FI-90570 Oulu, Finland.

[2]University of Helsinki, Department of Environmental Sciences, Section of Environmental Ecology, Niemenkatu 73, 15140 Lahti, Finland.

Correspondence: jani.heino@environment.fi

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Abstract

It was recently suggested that beta diversity can be partitioned into contributions of single sites to overall beta diversity (LCBD) or into contributions of individual species to overall beta diversity (SCBD). We explored the relationships of LCBD and SCBD to site and species characteristics, respectively, in stream insect assemblages. We found that LCBD was mostly explained by variation in species richness, with a negative relationship being detected. SCBD was strongly related to various species characteristics, such as occupancy, abundance, niche position and niche breadth, but was only weakly related to biological traits of species. In particular, occupancy and its quadratic terms showed a very strong unimodal relationship with SCBD, suggesting that intermediate species in terms of site occupancy contribute most to beta diversity. Our findings of unravelling the contributions of sites or species to overall beta diversity are of high importance to community ecology, conservation and bioassessment using stream insect assemblages, and may bear some overall generalities to be found in other organism groups.

Introduction

A major aim of ecology is to understand factors affecting spatial variation of species diversity. Species diversity can be divided into gamma, alpha and beta components (Whittaker 1960), of which the latter has received particular interest from ecologists in the last few years (Anderson et al. 2011). Recently, Legendre and De Cáceres (2013) suggested that beta diversity can be partitioned into contributions of single sites to overall beta diversity or into contributions of individual species to overall beta diversity. Hence, local contributions to beta diversity (LCBD) describe the ecological uniqueness of a site, whereas species contributions to beta diversity (SCBD) can be considered the relative importance of each species in affecting beta diversity patterns. A few studies have focused on LCBD to answer various questions of beta diversity (Lopes et al. 2014; Silva and Hernandes 2014; Tonkin et al. 2016), whereas correlates of SCBD have received little attention to date.

Patterns in LCBD and SCBD can be examined using site-based and species-based approaches, respectively. First, LCBD can be correlated with various environmental and spatial variables to see whether the ecological uniqueness of sites is based on environmental conditions (Lopes et al. 2014; Silva and Hernandes 2014; Tonkin et al. 2016), or result from community richness and abundance, which are, in turn, often determined by site environmental characteristics (Grönroos and Heino 2012; Tonkin et al. 2016). Second, SCBD can be associated with general species characteristics, such as degree of occupancy, abundance, niche position, niche breadth and species traits. These species characteristics have been shown to be inter-correlated at least to a certain degree (Tales et al. 2004; Heino 2005; Siqueira et al. 2009; Heino and Grönroos 2014). Also, as niche characteristics can be used to describe species-environment associations, they could be expected to be correlated with

SCBD. It can be assumed that generalist species with broad niches contribute less to SCBD than species with small or intermediate-sized niches. This is because species with small niche breadth may occur in environmentally restricted conditions (Brown 1984; Slatyer et al. 2013) and thus contribute more to beta diversity. Similarly, niche position can be assumed to be associated with SCBD because species occurring in marginal habitats should occur in environmentally more restricted conditions than non-marginal species (Dolédec et al. 2000; Heino and Grönroos 2014). Irrespective of niche characteristics, species biological traits, such as feeding mode, body size and dispersal capacity, might affect species contributions to beta diversity. This is because fundamental biological characteristics of species may affect species occupancy and abundance (Verberk et al. 2010; Heino and Grönroos 2014). The degree of occupancy should also itself affect SCBD, with species occurring at intermediate proportion of sites being most variable and contributing most to beta diversity. However, the effect of abundance may be different. Species having large total abundances in the data should also show most abundance variation among sites and thus show high contributions to beta diversity. These ideas are not completely new, as the mathematical relationship between mean, variance and occurrence is well known in ecological research (Gaston et al. 2006). However, these hypotheses remain to be tested rigorously, and they are important for understanding the formation of beta diversity patterns and revealing which kind of species, in terms of their ecological and biological traits, are particularly important.

We examined the contributions of single sites (LCBD) or single species (SCBD) to overall beta diversity in stream insect assemblages. Furthermore, we used community metrics (i.e. community richness and community abundance) and ecological variables (i.e. environmental features of the sites) as correlates of LCBD. Similarly, we used species metrics (i.e. species abundance and occupancy) and species characteristics (i.e. biological traits, niche position and niche breadth) as correlates of SCBD. We ran separate regression

models for community metrics and ecological features as predictors for variation in LCBD or SCBD. We used test data from three northern drainage basins showing wide variation in natural environmental conditions (Grönroos et al. 2013; Heino and Grönroos 2014). Previous studies from these and other drainage basins have shown that stream insects are highly amenable model organisms for testing the relationships between species and their environment (Heino 2005; Siqueira et al. 2009) and formation of biodiversity patterns (Heino et al. 2003; Hawkins et al. 2015). However, none of these studies has examined the correlates of LCBD or SCBD.

Materials and Methods

Study area and sampling

Stream insect samples were collected and environmental variables were measured in three drainage basins in Finland: Iijoki (65°N, 26°E; basin total area: 14 191 km^2), Koutajoki (66°N, 29°E; basin total area: 26 100 km^2) and Tenojoki (70°N, 27°E; basin total area: 16 374 km^2). Largely the same dataset has been used previously for examining community assembly (Heino 2013), metacommunity patterns (Grönroos et al. 2013), occupancy-abundance relationships (Heino and Grönroos 2014) and occupancy frequency patterns (Heino 2015) in stream invertebrates. Samples from altogether 60 near-pristine to pristine stream sites were included in the present study, with a total of 20 streams sampled in each of the three basins during the spring period. Thus, to ensure that the samples in each basin were collected at the same 'ecological season', the Iijoki samples were collected in late May in 2009, the Koutajoki samples were collected in late May 2008, and the Tenojoki samples were

109 collected in early to mid-June in 2010. We refer to the above mentioned papers for further
110 information about the study system.

111 At each site, approximately 100 m^2 stream riffle section was selected for sampling.
112 Macroinvertebrates were sampled using a kick-net (net mesh size 0.3 mm). Four 30-seconds
113 per one-meter subsamples were divided among the different microhabitats (based on
114 variation in velocity, depth, moss cover, and particle size) and pooled in the field. This
115 sampling effort should catch more than 70% of species occurring at a site, mainly missing
116 species that are only occasional in northern streams (Mykrä et al. 2006). Samples were
117 preserved in 70% ethanol in the field and later processed in the laboratory. Samples were
118 identified to species, species group, or genus level, including also non-biting midges
119 (Diptera: Chironomidae) and blackflies (Diptera: Simuliidae).

120 Altogether 15 environmental variables were measured at each site. Percentage cover
121 of deciduous trees (1) and canopy shading (2) were visually estimated along a 50 m stretch of
122 the riparian zone at each site on both banks. Mean riffle width (3) was measured at each
123 sampling site, based on five across-stream transects. Current velocity and depth were
124 measured at 30 random locations in cross-channel transects, the number of which depended
125 on riffle width. Moss cover (%) was visually estimated in ten randomly spaced 50 × 50 cm
126 plots. Mean current velocity (4), standard deviation of current velocity (5), mean depth (6),
127 standard deviation of depth (7), mean moss cover (8) and standard deviation of moss cover
128 (9) were then calculated and used in the analyses. Substratum particle size was visually
129 estimated from the same plots with moss cover estimates. In the analyses, we used the mean
130 percentage cover of the size classes sand (10), gravel (11), cobble (12) and bolder (13), which
131 correspond to diameters 0.25–2 mm, 2–16 mm, 64–256 mm and 256–1024 mm, respectively.
132 Conductivity (14) and pH (15) were measured either in laboratory using Finnish national

133 standards (National Board of Water and the Environment 1981) or using YSI device in the
134 field.

135

136 *Species traits, trait vectors and statistical analyses*

137

138 We gathered information for four biological traits/trait groups: functional feeding groups,
139 habit trait groups, body size and female dispersal strength. For functional feeding groups, we
140 mainly used Moog (2002) where one to 10 points are given for a species depending on its
141 association with each feeding group. Here, a species with ≥5 points for a given group was
142 assigned to belong to the respective group. For habit trait groups and female dispersal, we
143 mainly used US EPA (2012) trait database. Body size information was provided by S.
144 Dolédec (most groups), J. Ilmonen (Simuliidae) and L. Paasivirta (other dipterans). In cases
145 where the information was not found in the primary source, we also used Merritt and
146 Cummins (1996), Vieira et al. (2006), Tachet et al. (2010), taxonomic handbooks (e.g.
147 Nilsson 1996) and our expert opinion. There were five functional feeding groups (i.e.
148 predators = PRE, scrapers = SCR, filterers = FIL, gatherers = GAT and shredders = SHR),
149 five habit trait groups (i.e. clingers = CLIN, burrowers = BUR, sprawlers = SPR, climbers =
150 CLIM and swimmers = SWI; see Merritt and Cummins 1996), five body size classes (i.e.
151 maximum larval length coded as an ordered factor: 0-2.5 mm, 2.5-5 mm, 5-10 mm, 10-20
152 mm and 20-40 mm) and two female dispersal strength classes (i.e. low and high; see Poff et
153 al. 2006). We used this information on traits for calculating "trait distances" between species
154 based on Gower distance coefficient using the function "gowdis" from the R package *FD*
155 (Laliberté et al. 2014). We then ran a principal coordinates analysis (PCoA; based on the
156 Gower distances between species) using the function 'cmdscale' from the R package stats (R

157 core team 2015) to provide trait vectors for subsequent beta regression analyses. These trait
158 vectors are, contrary to the original trait variables, continuous variables that can be used to
159 describe trait differences between species (for a similar approach, see Heino and de Mendoza
160 2016). In practice, Euclidean distances between species based on the first four PCoA axes
161 and original Gower distances between species were very strongly correlated (Mantel $r = 0.909$, $p < 0.001$), indicating that the first four PCoA axes retained most of the information
163 about original trait distances between species.

164 We calculated niche position and niche breadth for each of the 203 species using the
165 outlying mean index (OMI) analysis (Dolédec et al. 2000). This method uses the relationships
166 between species abundances and environmental variables to produce three indices: 'OMI' or
167 the niche position of a species (NicPos), 'tolerance' or the niche breadth of a species
168 (NicBre), and 'residual tolerance' that helps one to infer how well environmental variables
169 considered have accounted for variation in species distributions. The OMI metric measures
170 the distance of each species to the average environmental conditions in the study area,
171 whereas the tolerance metric measures the amplitude in the species distributions across the
172 studied environmental gradients (Dolédec et al. 2000). Following Heino and Grönroos
173 (2014), we used all the 15 environmental variables to calculate realised environmental niche
174 position and environmental niche breadth for each species (analysis results shown in the
175 above mentioned paper). We calculated OMI and tolerance values for all species, including
176 very rare ones, as our community data analysis (see below) also incorporated all species. It
177 has to be noted, however, that species occurring at a single site only will get a value of 0 for
178 tolerance (NicBre). Although such zero values are unrealistic, as no species may have 'null'
179 niche breadth, they are useful in comparative purposes to indicate extreme species that have
180 very small niche breadth in a given study system.

We used a combination of multivariate methods and beta regression analysis to examine patterns in local contribution to beta diversity (LCBD) or species contributions to beta diversity (SCBD). Following Legendre and De Cáceres (2013), we first Hellinger-transformed site-by-species abundance or presence-absence community matrix, and subsequently calculated the total beta diversity (BD total), LCBD value for each site and SCBD value for each species. In brief, this approach is based on the total variance in the community matrix, which is the total sum of squares (the sum, over all species and all sites, of the squared deviations from the species means) divided by n-1. This measure, in turn, can be decomposed into the contribution of the sites or the species to total beta diversity (Legendre and De Cáceres 2013). For further details of calculating BD total, LCBD and SCBD values, and the R function 'beta.div' for conducting those calculations, see Legendre and De Cáceres (2013). LCBD represents the ecological uniqueness of a site, i.e. it provides a measure of the relative contribution of the given sampling unit to beta diversity. SCBD indicates how large a contribution a species has to overall beta diversity in the data set. Large LCBD or large SCBD values indicate high importance of the given site or species, respectively, to the overall beta diversity (i.e. variation in species composition across sites; Anderson et al. 2011). We ran the analysis using both abundance and presence-absence data to show if there were differences between quantitative and qualitative data.

We used Kruskal-Wallis test (R function 'kruskal.test') and associated multiple comparisons (R function 'kruskalmc') to test for pairwise differences in both LCBD measures as well as community richness and community abundance among the three drainage basins. Pairwise comparisons were based on the method developed by Siegel and Castellan (1988, pp. 213-214). Kruskal-Wallis test was selected for these comparisons because our data did not meet all assumptions of parametric tests (i.e. ANOVA).

Because our response data (LCBD or SCBD) varied between 0 and 1, we used beta regression as our modelling tool (Cribari-Neto and Zeileis 2010). Beta regression is typically used to model variables that show values in the standard unit interval (i.e. vary between 0 and 1). Beta regression is based on the assumption that the dependent variable is beta-distributed and that its mean is related to a set of regressors through a linear predictor with unknown coefficients and a link function (Cribari-Neto and Zeileis 2010). The beta regression approach naturally incorporates features such as heteroskedasticity or skewness which are typically observed in response data taking values from 0 to 1. We used beta regression with logit link function for four separate models. First, we related LCBD to community metrics, namely species richness and community abundance, as well as their second order terms to account for nonlinear responses (Supporting information, Fig. S1). Second, we ran beta regression of LCBD using eight main environmental variables as predictors (i.e. pH, conductivity, shading, riparian deciduous trees, stream width, depth, velocity and moss cover). These variables have formerly been found to be influential in affecting variation in macroinvertebrate communities in northern streams (Grönroos and Heino 2012; Heino et al. 2014). Third, we used beta regression to relate SCBD to species metrics, including number of sites occupied (NumSit), total abundance of a species in the dataset (TotAbu), as well as their quadratic terms (Supporting information, Fig. S1). Finally, in the fourth model, we used beta regression to analyse variation in SCBD using niche position (NicPos), niche breadth (NicBre), and the first four PCoA trait vectors as predictor variables (see above). We also examined reduced models based on pseudo coefficients of determination (pseudo-R^2).

Statistical analyses, except calculations of local or species contributions to beta diversity, were run using the R packages stats (R Core Team 2015), ade4 (Dray and Dufour 2007), pgirmess (Giraudoux 2016) and betareg (Cribari-Neto and Zeileis 2010).

Results

Total beta diversity numbers were 38.67 for SS total and 0.655 for BD total based on presence-absence data. Corresponding figures for abundance data were 37.57 for SS total and 0.636 for BD total.

LCBD based on presence-absence data was significantly related to community richness and its quadratic term, but not with community abundance (Table 1). Abundance-based LCBD was significantly related to community abundance. Also, none of the environmental variables was strongly related to LCDB, although the variable "deciduous trees" was significant in the model of abundance-based LCBD (Table 2). Also, pseudo R^2 values of these models were low. However, there were significant differences in abundance-based LCBD, community richness and community abundance among the three drainage basins (Kruskal-Wallis test, $p < 0.05$), but no significant differences were found for presence-absence LCBD. Based on multiple comparisons in Kruskal-Wallis test ($p < 0.05$), lower community richness was found in streams of the Tenojoki basin than in the Iijoki and Koutajoki basins. Also, community abundance was higher in the Iijoki basin than in the other two basins, and abundance-based LCBD was higher in the Koutajoki basin than in the Tenojoki basin (Fig. 1).

SCBD based on presence-absence data was significantly related to number of sites occupied and its quadratic term, but not with total abundance and its quadratic term (Table 3). The model including all four explanatory variables (i.e. number of sites occupied and its quadratic term, total abundance and its quadratic term) accounted for 85% of variation in SCBD. In addition, the model that included only the variable 'number of sites occupied' and its quadratic term accounted for 85% of variation in SCBD, and a hump-shaped relationship between the number of sites occupied and SCBD was observed (Fig. 2, Supporting

information Fig. S1). SCBD based on abundance data showed rather similar patterns to those of presence-absence data. However, in this model, total abundance and its quadratic term were also significant (Table 3). The model including all explanatory variables accounted for 72% of variation. The model that only included number of sites occupied as well as its quadratic term, however, explained 63% of variation in abundance-based SCBD (Fig. 2). Beta regression also showed that SCBD-trait relationships were rather weak (Table 4), and only niche position explained significant variation in both SCBD indices. However, niche breadth was also significant predictor of SCBD based on presence-absence data, and pco3 was also significantly related to variation in SCBD based on abundance data (Table 4). This trait vector was related to variation in functional feeding mode (scrapers had high values and predators had low values), habit traits (high values for sprawlers and low values for burrowers), body size (small size classes had high values and large size classes had low values) and female dispersal potential (low dispersal had higher values than high dispersal) (Fig. 3). Inspection of the relationships between SCBD indices and original trait variables showed that female dispersal capacity was most clearly associated with species contribution to beta diversity (Supporting Information Fig. S3).

One species, the mayfly *Baetis rhodani*, had a very high Cook's distance in SCBD-related beta regression analyses. This species was the most abundant and was among the three most widely distributed species in the dataset. Its removal did not appreciably affect the interpretation of the results and it was thus included in the model. Also, when this species was excluded, a few other species appeared to have high Cook's distance.

Discussion

Our findings showed that both local contribution to beta diversity (LCBD) and species contribution to beta diversity (SCBD) showed some highly predictable patterns. First, LCBD was significantly related to species richness, whereas SCBD showed significant relationships with various species metrics, particularly with number of sites occupied by a species. However, environmental variables were less influential for LCBD, and the same was true for species traits for SCBD. In the following, we will discuss these main findings.

We found that LCBD was negatively related to species richness, although the relationship was also slightly curvilinear (Table 1a). Legendre and De Cáceres (2013) and Silva and Hernandez (2014) also found that LCBD was negatively correlated with species richness, indicating that sites with unique species composition harboured low species richness. However, in our analyses, when LCBD was based on abundance data, the relationship between LCBD and species richness was not significant, but community abundance was significant (Table 1b). Our findings thus suggest that the variation in LCBD of stream insects across streams is governed by variation in species richness or abundance (depending on whether presence-absence or abundance data are used in the calculation of LCBD), which in turn may be typically correlated with factors such as stream size, moss cover and pH or vary between drainage basins (Heino et al. 2003; Heino and Grönroos 2012). However, we did not find among-drainage basin differences in LCBD based on presence-absence data, although abundance-based LCBD, species richness and community abundance did show significant differences. This finding further suggests that both local stream-level factors and drainage basin identity may affect LCBD, but these relationships may be complex (cf. presence-absence vs. abundance-based LCBD results). Also, in this study, the variation in LCBD values was not explained well by local environmental variables. This finding is rather similar to that of Tonkin et al. (2016), who found that LCBD was variably related to environmental factors in five different stream invertebrate datasets.

303 SCBD correlated significantly with the species metrics, notably with the number of
304 sites occupied and its quadratic term. These two variables alone explained 85% and 68% of
305 variation in presence-absence and abundance-based SCBD, respectively, but shape of the
306 relationship was different (Fig. 2). Our findings showed, in the presence-absence case, that
307 intermediate species in terms of site occupancy contribute most to the presence-absence-
308 based beta diversity. This is because those intermediate species show most variation in
309 occupancy among sites (see also Gaston et al. 2006). Our results also showed, in the
310 abundance case, that species with high occupancy across sites and high total abundance in the
311 data contribute most to the abundance-based beta diversity. The finding that widely-
312 distributed species are also abundant relates to the positive occupancy-abundance relationship
313 (Brown 1984; Gaston 2003), which has also been detected previously in stream ecosystems in
314 general (e.g. Siqueira et al. 2009) and the present study system in particular (e.g. Heino and
315 Grönroos 2014). Our findings also suggest that species contribution to beta diversity in a
316 dataset is strongly predictable from general species characteristics, including its occupancy
317 and abundance. This is somewhat circular reasoning, however, as SCBD, occupancy and
318 abundance are calculated from the same data. This mathematical dependency may affect the
319 relationships among occupancy, abundance and SCBD (see also Legendre and De Cáceres
320 2013). For example, high SCBD values mean that species show a large variation in
321 abundance across locations. The mean-variance relation suggests that such species are
322 expected to have relatively high local abundance as well as high occurrence. Similarly, if we
323 measure SCBD using species presence-absence data, high variance is shown by species that
324 have intermediate occurrence.

325 We found only weak effects of species traits on SCBD. While niche position was a
326 significant determinant of SCBD in both cases, niche breath was significant only for SCBD
327 based on presence-absence data, and only the third PCoA axis was significantly related with

328 variation in SCBD based on abundance data. This finding suggests that biological traits are
329 less important than niche position in affecting SCBD. This finding is not surprising because
330 niche position is typically strongly correlated with occupancy (Heino 2005; Siqueira et al.
331 2009), and hence could be assumed to be related to SCBD. Also, niche position is related to
332 the amount of variability in the occupancy of species that can be accounted for by
333 environmental variables (Heino and de Mendoza 2016). This suggests that there may be
334 complex, yet predictable relationships between SCBD, occupancy, niche position and
335 environmental relationships of species. Biological traits fit less well into this equation, as
336 they were not strongly related to either SCBD (this study) or species occupancy (Heino and
337 de Mendoza 2016). However, one biological trait PCoA axis was significantly related to
338 SCBD based on abundance data, which suggests that their role cannot be entirely ruled out.
339 In this context, female dispersal capacity may be a key trait, with low dispersal capacity
340 being probably related to high contribution to beta diversity (Supporting information Fig. S3).

341 Understanding the determinants of LCBD and SCBD is important from basic
342 ecological, conservation and bioassessment viewpoints. First, LCBD indicates the ecological
343 uniqueness of a site (Legendre and De Cáceres 2013), which goes beyond typical measures of
344 beta diversity and provides a means to value single sites separately. Second, valuing single
345 sites is important for conservation because limited resources do not allow us to conserve all
346 sites. Therefore, preserving a set of ecologically unique sites is one option for biodiversity
347 conservation. However, one has to consider that sites having high LCBD values are often
348 rather species poor sites (Legendre and De Cáceres 2013; Silva and Hernandes 2014), which
349 may limit their use in conservation if species-rich sites are a conservation goal. A
350 compromise would be to conserve a combined set of both ecologically unique and species-
351 rich sites. Third, from the bioassessment perspective, it would be feasible to focus on species
352 having intermediate site occupancy, as these species contribute most to beta diversity.

353 Changes in the occupancies of these species should also result in clearly discernible changes
354 in the variation of community structure across sites in the face of anthropogenic changes.
355 This is particularly so if previously uncommon species 'switch roles' with previously widely-
356 distributed or highly abundant species. For example, Hawkins et al. (2015) found that
357 anthropogenic disturbances decreased the regional prevalence of most common taxa and
358 increased the prevalence of several less common taxa in stream macroinvertebrate
359 communities. This finding also suggests that species contributions to beta diversity change
360 with anthropogenic disturbance, resulting in biodiversity patterns differing between sets of
361 anthropogenically altered and more pristine ecosystems (but see Mayor et al. 2015).

362 In conclusion, we found that LCBD and SCBD were highly predictably related to
363 species richness and species occupancy, respectively. We emphasise the importance of SCBD
364 in this context, as the contributions of single species to overall beta diversity have been little
365 studied using this approach. At the same time, understanding the determinants of LCBD and
366 SCBD may hold a key to various general ecological, conservation and bioassessment issues.
367 We thus urge other researchers to test the generality of our findings in ecological systems
368 other than running waters.

369

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371

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References

Anderson MJ, Crist TO, Chase JM, Vellend M, Inouye BD, Freestone AL, Sanders NJ, Cornell HV, Comita LS, Davies KF, Harrison SP, Kraft NJB, Stegen JC, Swenson GS (2011) Navigating the multiple meanings of β diversity: a roadmap for the ecologist. Ecol Lett 14:19-28

Brown JH (1984) On the relationship between abundance and distribution of species. Am Nat 124: 255-279.

Cribari-Neto F, Zeileis A (2010) Beta Regression in R. J Statistical Softw 34:1-24

Dolédec S, Chessel D, Gimaret-Carpentier C 2000. Niche separation in community analysis: a new method. Ecology 81:2914–2927

Dray S, Dufour AB (2007): The ade4 package: implementing the duality diagram for ecologists. J Statistical Softw 22: 1-20

Gaston KJ (2003) The structure and dynamics of geographic ranges. Oxford University Press, Oxford

Gaston KJ, Borges PAV, He F, Gaspar C (2006) Abundance, spatial variance and occupancy: arthropod species distribution in the Azores. J Anim Ecol 75:646–656

Giraudoux P (2016) pgirmess: Data Analysis in Ecology. R package version 1.6.4. http://CRAN.R-project.org/package=pgirmess

397 Grönroos M, Heino J (2012) Species richness at the guild level: effects of species pool and
398 local environmental conditions on stream macroinvertebrate communities. J Anim
399 Ecol 81:679-691

400 Grönroos M, Heino J, Siqueira T, Landeiro VL, Kotanen J, Bini LM (2013) Metacommunity
401 structuring in stream networks: roles of dispersal mode, distance type and regional
402 environmental context. Ecol Evol 3:4473-4487

403 Hawkins CP, Mykrä H, Oksanen J, Vander Laan JJ (2015) Environmental disturbance can
404 increase beta diversity of stream macroinvertebrate assemblages. Glob Ecol
405 Biogeogr 24: 483–494

406 Heino J (2005) Positive relationship between regional distribution and local abundance in
407 stream insects: a consequence of niche breadth or habitat niche position? Ecography
408 28: 345-354.

409 Heino J (2013) Environmental heterogeneity, dispersal mode, and co-occurrence in stream
410 macroinvertebrates. Ecol Evol 3:344–355

411 Heino J (2015) Deconstructing occupancy frequency distributions in stream insects: effects of
412 body size and niche characteristics in different geographical regions. Ecol Entomol
413 40:491-499

414 Heino J, Grönroos M (2014) Untangling the relationships among regional occupancy, species
415 traits and niche characteristics in stream invertebrates. Ecol Evol 4:1931-1942

416 Heino J, Ilmonen J, Paasivirta L (2014) Continuous variation of macroinvertebrate
417 communities along environmental gradients in northern streams. Boreal Env Res
418 19:21-38

419 Heino J, Muotka T, Paavola R (2003) Determinants of macroinvertebrate diversity in
420 headwater streams: regional and local influences. J Anim Ecol 72:425-434

421 Laliberté E, Legendre P, Shipley B (2014) FD: measuring functional diversity from multiple
422 traits, and other tools for functional ecology. R package version 1.0-12

423 Legendre P, De Cáceres M (2013) Beta diversity as the variance of community data:
424 dissimilarity coefficients and partitioning. Ecol Lett 16:951-963

425 Lopes PM, Bini LM, Declerck SAJ**,** Farjalla V F, Vieira LCG, Bonecker CC, Lansac-Toha
426 FA, Esteves FA, Bozelli RL (2014) Correlates of zooplankton beta diversity in
427 tropical lake systems. PLoS ONE 9:e109581

428 Mayor SJ, Boutin S, He F, Cahill JF Jr (2015) Limited impacts of extensive human land use
429 on dominance, specialization, and biotic homogenization in boreal plant
430 communities**.** BMC Ecology 15:5

431 Merritt RW, Cummins KW (1996) An introduction to the aquatic insects of North America,
432 third edition. Kendall/Hunt

433 Mykrä H, Ruokonen T, Muotka T (2006) The effect of sample duration on the efficiency of
434 kick-sampling in two streams with contrasting substratum heterogeneity. Ver Int Ver
435 Theor Ang Limnol 29:1351–1355

436 National Board of Waters and the Environment 1981. Vesihallinnon analyysimenetelmät. –
437 Publ. Nat. Board Wat. Finland. Report 213:1–136

438 Nilsson A (ed.) (1997) Aquatic insects of North Europe, Volume 2. Apollo Books, Stenstrup

439 Poff NL, Olden JD, Vieira NKM, Finn DS, Simmons MP, Kondratieff BC (2006) Functional
440 trait niches of North American lotic insects: traits-based ecological applications in
441 light of phylogenetic relationships. J N Amer Bentholl Soc 25:730-755

442 R Core Team (2015) R: A language and environment for statistical computing. R Foundation
443 for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/

444 Siegel S, Castellan NJ (1988) Nonparametric statistics for the behavioural sciences.
445 MacGraw Hill International, New York

446 Silva PG da, Hernández MIM (2014) Local and Regional Effects on Community Structure of
447 Dung Beetles in a Mainland-Island Scenario. PLoS ONE 9:e111883

448 Siqueira T, Bini LM, Cianciaruso MV, Roque FO, Trivinho-Strixino S (2009) The role of
449 niche measures in explaining the abundance–distribution relationship in tropical lotic
450 chironomids. Hydrobiologia 636:163-172

451 Slatyer, R.A., Hirst, M. & Sexton, J.P. (2013) Niche breadth predicts geographical range size:
452 a general ecological pattern. Ecol Lett 16: 1104–1114

453 Tachet H, Richoux P, Bournaud M, Usseglio-Polatera P (2010) Invertébrés d'eau douce:
454 systématique, biologie, écologie (nouvelle édition revue et augmentée). CNRS, Paris

455 Tales E, Keith P, Oberdorff T (2004) Density-range size relationships in French riverine
456 fishes. Oecologia 138:360–370

457 Tonkin JD, Heino J, Sundermann A, Haase P, Jähnig S (2016) Context dependency in
458 biodiversity patterns of central German stream metacommunities. Freshwater Biol 61:
459 607-620

460 U.S. EPA. Freshwater Biological Traits Database (Final Report) (2012) U.S. Environmental
461 Protection Agency, Washington, DC, EPA/600/R-11/038F, 2012

462 Verberk WCEP, van der Velde G, Esselink H (2010) Explaining abundance-occupancy
463 relationships in specialists and generalists: a case study on aquatic macroinvertebrates
464 in standing waters. J Anim Ecol 79: 589-601

Vieira NKM, Poff N, Carlisle DM, Moulton SR, Koski ML, Kondratieff BC, (2006) A database of lotic invertebrate traits for North America: U.S. Geological Survey Data Series 18

Whittaker RH (1960) Vegetation of the Siskiyou Mountains, Oregon and California. Ecol Monogr 30:279–338

Tables

Table 1. Results of beta regression analyses when the response variable, local contributions to beta diversity (LCBD), was explained by community metrics (i.e. community richness and abundance, and their quadratic terms). Both (a) presence-absence and (b) abundance data were used for calculating LCBD.

a) LCBD p-a	Estimate	SE	z	p		Model Pseudo-R^2
(Intercept)	-3.394	0.130	-26.035	0.000	***	
Richness	-0.041	0.010	-3.895	0.001	***	
Richness^2	0.001	0.000	3.380	0.001	***	
Abundance	-0.000	0.000	-1.487	0.137		
Abundance^2	0.000	0.000	1.393	0.164		0.368

b) LCBD abund.	Estimate	SE	z	p		Model Pseudo-R^2
(Intercept)	-3.748	0.210	-17.860	0.000	***	
Richness	-0.020	0.016	-1.249	0.212		
Richness^2	0.001	0.000	1.758	0.079		
Abundance	-0.001	0.000	-12.127	0.003	*	
Abundance^2	0.000	0.000	1.654	0.098		0.166

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Table 2. Results of beta regression analyses when the response variable, local contributions to beta diversity (LCBD), was explained by local environmental variables. Both (a) presence-absence and (b) abundance data were used for calculating LCBD.

a) LCBD p-a	Estimate	SE	z	p		Model Pseudo-R^2
(Intercept)	-3.459	0.631	-5.479	0.000	***	
pH	-0.054	0.093	-0.577	0.564		
Conductivity	0.005	0.014	0.367	0.714		
Shading	0.000	0.001	0.059	0.953		
Deciduous trees	-0.000	0.000	-0.977	0.329		
Stream width	-0.000	0.000	-0.557	0.577		
Depth	-0.002	0.003	-0.762	0.446		
Velocity	-0.270	0.151	-1.790	0.073		
Macrophytes	-0.002	0.001	-1.546	0.122		0.113

b) LCBD abund.	Estimate	SE	z	p		Model Pseudo-R^2
(Intercept)	-3.654	0.772	-4.732	0.000	***	
pH	-0.037	0.113	-0.326	0.745		
Conductivity	0.023	0.016	1.402	0.161		
Shading	-0.000	0.001	-0.571	0.568		
Deciduous trees	-0.003	0.001	-2.536	0.011	*	
Stream width	-0.000	0.000	-0.141	0.888		
Depth	0.002	0.004	0.494	0.621		
Velocity	-0.195	0.186	-1.049	0.294		
Macrophytes	-0.001	0.002	-0.634	0.526		0.217

Table 3. Results of beta regression analyses when species contributions to beta diversity (SCBD) was explained by species metrics. Both (a) presence-absence and (b) abundance data were used to calculate SCBD. NumSit = number of sites occupied, TotAbu = a species total abundance in the dataset.

a) SCBD p-a	Estimate	SE	z	p		Model Pseudo-R^2
(Intercept)	-6.598	0.049	-134.450	0.000	***	
NumSit	0.171	0.006	29.422	0.000	***	
$NumSit^2$	-0.003	0.000	-18.757	0.000	***	
TotAbu	0.000	0.000	-0.024	0.981		
$TotAbu^2$	0.000	0.000	1.153	0.249		0.851

b) SCBD abund.	Estimate	SE	z	p		Model Pseudo-R^2
(Intercept)	-7.186	0.107	-66.911	0.000	***	
NumSit	0.141	0.009	15.563	0.000	***	
$NumSit^2$	-0.002	0.000	-11.513	0.000	***	
TotAbu	0.002	0.000	11.248	0.000	***	
$TotAbu^2$	-0.000	0.000	-9.521	0.000	***	0.717

Table 4. Results of beta regression analyses when species contributions to beta diversity (SCBD) was explained by species ecological and biological traits. Both (a) presence-absence and (b) abundance data were used to calculate SCBD. NicPos = Niche position, NicBre = Niche breadth. Niche characteristics were derived from the OMI analysis, and the first four PCoA axes (pco1-pco4) were used as synthetic trait vectors.

a) SCBD p-a						Model
	Estimate	SE	z	p		Pseudo-R^2
(Intercept)	-4.698	0.056	-83.801	0.000	***	
Niche position	-0.125	0.006	-21.616	0.000	***	
Niche breadth	0.084	0.018	4.612	0.001	***	
pco1	-0.060	0.109	-0.553	0.580		
pco2	0.098	0.174	0.567	0.571		
pco3	0.299	0.179	1.666	0.096		
pco4	0.164	0.205	0.802	0.423		0.395

a) SCBD abund.						Model
	Estimate	SE	z	p		Pseudo-R^2
(Intercept)	-5.085	0.125	-40.791	0.000	***	
Niche position	-0.042	0.007	-6.359	0.000	***	
Niche breadth	0.053	0.034	1.583	0.113		
pco1	-0.283	0.206	-1.370	0.171		
pco2	0.106	0.322	0.328	0.743		
pco3	0.773	0.340	2.275	0.023	*	
pco4	0.098	0.392	0.250	0.802		0.288

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Figure legends

Fig. 1. Difference in local contributions to beta diversity (LCBD) (a, b), community richness (c) and community abundance (d) among the three drainage basins. Note that there was much variation within each basin in LCBD values, even though community richness and abundance also varied clearly among the basins. II=Iijoki basin, KO=Koutajoki basin, TE=Tenojoki basin. Twenty sites were surveyed in each basin

Fig. 2. Relationship between species contribution to beta diversity (SCBD) based on presence-absence data (a) or abundance data (b) and number of sites occupied by species. N = 203 species

Fig. 3. Relationships between the first four PCoA axes (pco1-pco4) and the four trait variables. FFG = functional feeding group, HTG = habit trait group, SIZE = maximum larval body length, and FDISP = female dispersal potential. See text for individual trait abbreviations

Fig. 1.

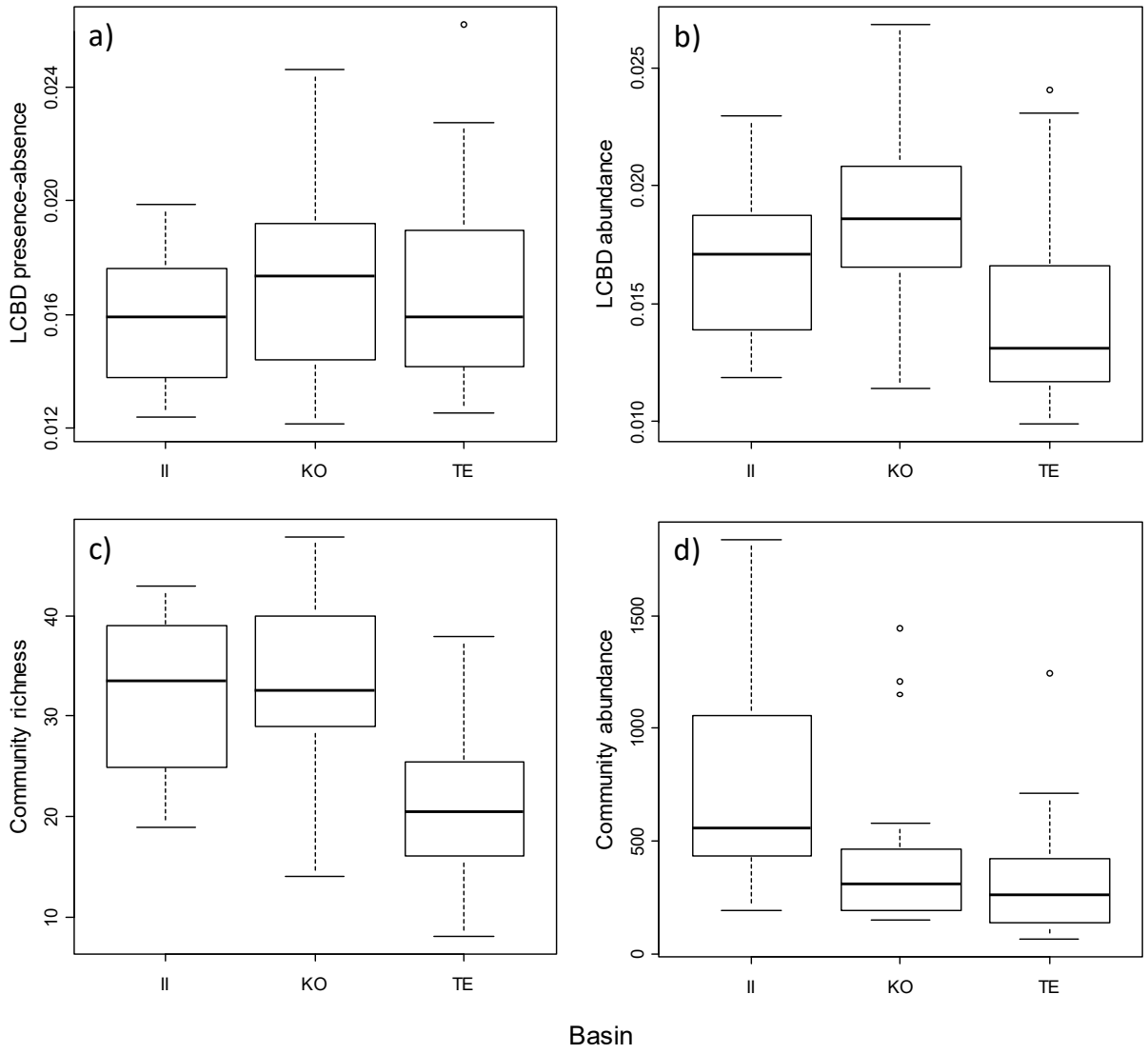
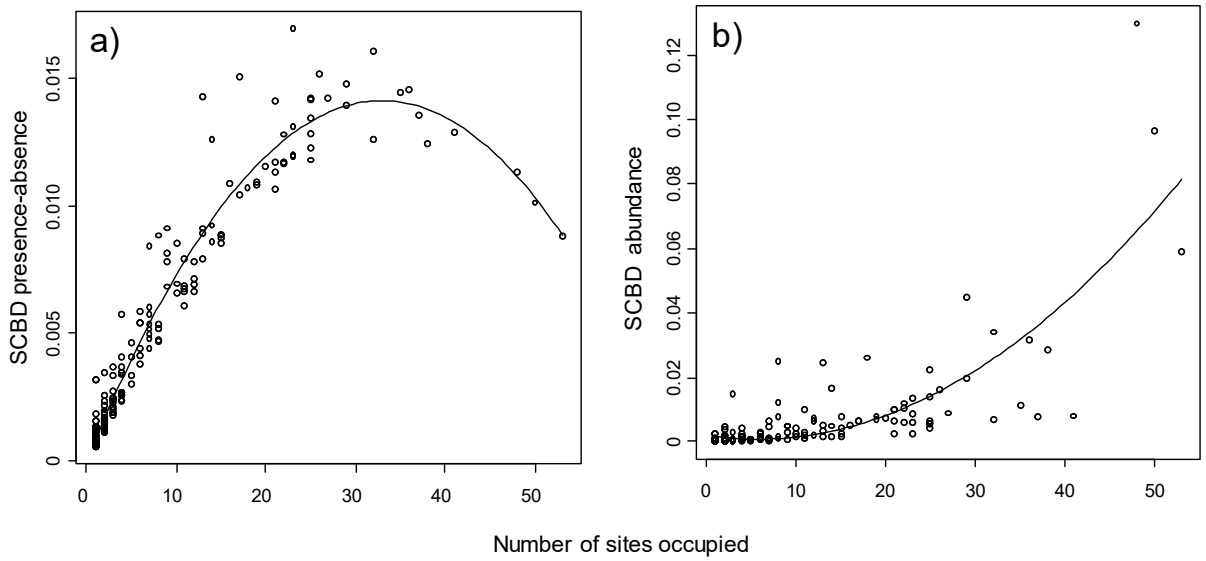
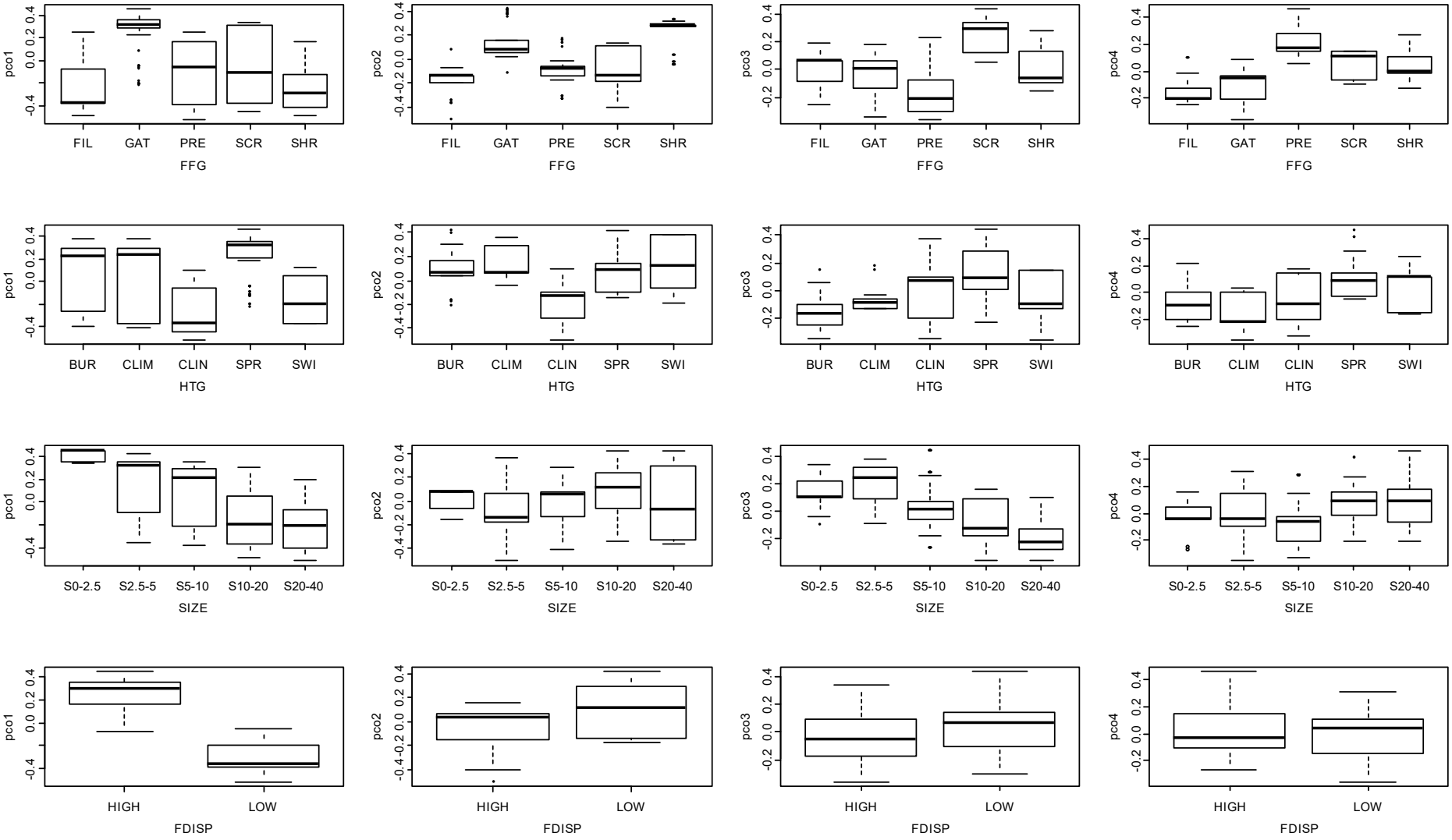

a)
LCBD presence-absence
0.012
0.016
0.020
0.024
Il
KO
TE
b)
LCBD abundance
0.010
0.015
0.020
0.025
Il
KO
TE
c)
Community richness
10
20
30
40
Il
KO
TE
d)
Community abundance
0
500
1000
1500
Il
KO
TE
Basin

Fig. 2.


a)
b)
SCBD presence-absence
SCBD abundance
0
0.005
0.010
0.015
0.02
0.04
0.06
0.08
0.10
0.12
0
10
20
30
40
50
Number of sites occupied

473 Fig. 3.


pco1
pco2
pco3
pco4
-0.4
0.0
0.2
0.4
FIL
GAT
PRE
SCR
SHR
FFG
BUR
CLIM
CLIN
SPR
SWI
HTG
S0-2.5
S2.5-5
S5-10
S10-20
S20-40
SIZE
HIGH
LOW
FDISP

474